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(Article begins on next page)

# **Structural and environmental constraints on paired appendages reduction among vertebrates**

LOREDANA MACALUSO<sup>1\*</sup>, GIORGIO CARNEVALE<sup>1</sup>, RAFFAELLO CASU<sup>2</sup>, DANIEL  
PIETROCOLA<sup>1</sup>, ANDREA VILLA<sup>3,1</sup> and MASSIMO DELFINO<sup>1,4</sup>

<sup>1</sup>Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, 10125, Torino, Italy

<sup>2</sup> Dipartimento di Fisica, Università degli Studi di Torino, Via Pietro Giuria 1, 10125, Torino, Italy

<sup>3</sup> Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 München, Germany

<sup>4</sup> Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici Z (ICTA-ICP), Carrer de les Columnes s/n, Campus de la UAB, E-08193 Cerdanyola del Valles, Barcelona, Spain

\*Corresponding author. E-mail: [loredana.macaluso@unito.it](mailto:loredana.macaluso@unito.it)

## ABSTRACT

Burrowing habits or complex environments have been generally considered as potential drivers acting on appendicular skeleton reduction and loss among vertebrates. Herein we suggest that this may be the case for lissamphibians and squamates, but that fin loss in fishes is usually prevented due to important structural constraints, as pectoral fins are commonly used to control rolling and pitching. We provide an overview of the distribution of paired appendage reduction across vertebrates while examining the ecological affinities of finless and limbless clades. We analysed the correlation between life style and fin or limb loss using the discrete comparative analysis. The resulting Bayesian Factors indicate a strong evidence of correlation between: (i) pectoral-fin loss and coexistence of anguilliform elongation and burrowing habits or complex habitat in teleost fishes, and (ii) limb loss and burrowing or grass-swimming life style in squamate reptiles and lissamphibians. These correlations suggest that a complex environment or a fossorial habit constitute driving forces leading to appendage loss. The only locomotion style that is functional even in absence of paired appendages is the undulatory one, which is typical of all elongated reptiles and lissamphibians, but certainly less common in teleost fishes.

ADDITIONAL KEYWORDS: limb loss – eel-like fishes – elongated tetrapods – comparative phylogenetic analyses – amphibians – reptiles

## INTRODUCTION

Reduction or loss of the appendicular skeleton occurred multiple times in representatives of several fish and tetrapods lineages. Among extant tetrapod classes (Moyle & Cech, 2003; Vaughan *et al.*, 2011; Pough *et al.*, 2015; Morrison *et al.*, 2018), extreme reduction or loss of limbs occurred in mammals (cetaceans and sirenians), birds (moa and kiwi), squamate reptiles (snakes, amphisbaenians and several groups of lizards) and “amphibians” (the Carboniferous-Permian aistopods and the lissamphibian caecilians plus a few groups of salamanders), whereas the loss of paired fins has been observed in several groups of teleost fishes. Even though in both mammals and birds, reduction and skeletal loss affect alternatively the forelimbs or hindlimbs only, there are several groups of squamate reptiles, amphibians and teleost fishes that exhibit a complete absence of paired limbs or fins. Despite these groups are phylogenetically distant, they all share some similarities. First of all, squamate reptiles, lissamphibians and teleosts characterized by a reduction of the appendicular skeleton usually exhibit an elongated body (Gans, 1975; Ward & Mehta, 2010 and references therein). According to Greer (1991), there are fifty-three squamate lineages that have undergone limb reduction, distributed among Agamidae, Amphisbaenia, Anguidae, Anniellidae, Chamaleonidae, Cordylidae, Dibamidae, Diploglossidae, Gekkota, Gerrhosauridae, Helodermatidae, Lanthanotidae, Ophidia, Pygopodidae, Scincidae and Teiidae. The situation is different among lissamphibians as, although different groups exhibit an elongated body, only three lineages show appendages reduction or loss. Caecilians (Gymnophiona) are the only lissamphibians characterized by a complete loss of both fore- and hindlimbs. Members of Sirenidae, on the other hand, have lost the hindlimbs, but retain reduced forelimbs. In the end, the only genus included within Amphiumidae, *Amphiuma*, has very short and motionless limbs. Among extinct basal tetrapods, the Carboniferous-Permian Aistopoda are completely limbless, showing a remarkable convergence with the serpentiform body plan of snakes and caecilians (Carroll *et al.*, 1998; Pardo & Mann, 2018). In general, all the elongated squamates and lissamphibians exhibit a similar lateral undulation even if using different types of locomotion (Gans, 1975). Conversely, elongated fishes exhibit carangiform or anguilliform locomotion (Sfakiotakis *et al.*, 1999, Horner & Jayne, 2008; Pfaff *et al.*, 2016). If the carangiform pattern is characterized by more or less rigid movements of the caudal portion of the body and tail, the anguilliform pattern is characterized by a sinuous wave that moves

through the body (e.g., eels) or only in its posterior part (e.g., catfishes). The anguilliform movement, which could be associated to the “serpent-like” movement of tetrapods, is typical of at least half of the highly elongated actinopterygians (Ward & Mehta, 2010; Reece & Mehta, 2013). In particular, anguilliform elongation (*sensu* Ward & Mehta, 2010) is typical of *Erpetoichthys calabaricus* among Polypteriformes (Suzuki *et al.*, 2010), some members of the clades Ophidiiformes, and Gobionellidae (genus *Luciogobius*; Yamada *et al.*, 2009), and most of the members of the clade Anguilliformes, Lampridiformes, Mastacembelidae, and Zoarcales (Ward & Mehta, 2010). Some elongated members of the clades Ateleopodiformes, Liparidae, and Siluriformes show a body plan with an enlarged, heavy head and their anguilliform movement is limited to the posterior part of the body (i.e., not including the pectoral area). The pelvic fins are lost in several, morphologically different groups of fishes, in more than 90 teleost lineages (Nelson, 1989; Kriwet & Pfaff, 2019), whereas the pectoral fins are primarily lost in elongated fishes with anguilliform locomotion (Mehta *et al.*, 2010). Eel-like clariid species represent a unique case among vertebrates, as their paired fins show a very high intraspecific level of morphological variability, preventing their absence to be used as a diagnostic feature at the species level (Devaere *et al.*, 2004). As in other vertebrates (O'Reilly *et al.*, 1997), the loss of fins in clariids was regarded as related to a highly specialized fossorial mode of life by Devaere *et al.* (2004), although this hypothesis has not been tested yet. More generally, the idea that the presence of appendages may represent an impediment for burrowing for both terrestrial and aquatic animals is widely accepted. Recently, Da Silva *et al.* (2018) demonstrated that fossoriality has been the evolutionary driver leading to the origin and development of the snake body plan. Extinct relatives of extant limbless forms (e.g., amphisbaenians and caecilians) indicate that fossoriality evolved before the limb loss since they have cranial adaptations for burrowing, but maintain variably developed appendages (Evans & Sigogneau-Russell, 2001; Jenkins *et al.*, 2007; Talanda, 2016). Nevertheless, fossoriality is not the only evolutionary driver for limb loss in reptiles, and limbless squamates are traditionally divided into short-tailed burrowers or long-tailed surface dwellers, moving through loose sand or vegetation (Evans, 1998; Wiens *et al.*, 2006).

As far as fishes are concerned, it is known that a number of fishes exhibiting an eel-like body morphology are either crevice-dwellers or burrowers (tail- or head-first; De Schepper *et al.*, 2007a, b; Herrel

*et al.*, 2011). Nevertheless, previous studies mainly focused on the correlation between elongation and habitat, or trophic adaptations (Ward & Mehta, 2010; Mehta *et al.*, 2010; Claverie & Wainwright, 2014), but did not find any apparent connection. Mehta *et al.* (2010), in particular, stated that, although it is generally true that terrestrial vertebrates evolved an elongated, limb-reduced body plan as an adaptation for the burrowing lifestyle, little is known about how much the elongate body form may be adapted for aquatic habits.

Herein we suggest that a distinction can be done in fishes between anguilliform and stiffer-body elongation (*sensu* Ward & Mehta, 2010) when studying correlations between habitat and body plan, as the constraints due to balance problem during swimming connected with these two body forms are different. Moreover, we attempt to address the question: once a fish has evolved an eel-like elongation, does the habitat have an influence on paired-fins loss? Is there a common trend in appendage loss in teleosts and tetrapods? Herein, we argue that the limbless body plan in vertebrates is affected by similar environmental constraints, provided by the habitat or life style, and we try to summarize how widespread this pattern (i.e. dense, complex environment acting on appendage reduction and loss) actually is.

## GENETIC AND DEVELOPMENTAL CONTROL OF APPENDAGE LOSS

The development of appendages is polygenic, involving genes with pleiotropic effects (Lande, 1978; Hall, 2008). Therefore, genes involved in limbs and paired fins development also function on other developing systems, such as jaws or genitals (Rosa-Molinar & Burke, 2002). This is the reason why genes associated with limb buds are generally not lost, even in limbless forms (Bejder & Hall, 2002). The developmental mechanism of the formation of paired appendages is deeply conserved among gnathostomes (Dahn *et al.*, 2007; Letelier *et al.*, 2018) and it involves two signalling centers located in the fin/limb bud. The first of them is the apical ectodermal ridge (AER), which helps to maintain the second one, the zone of polarizing activity (ZPA), the cells of which express the Sonic hedgehog (Shh) gene, associated with the development of the fins or limbs (Cohn, 2001; Bejder & Hall, 2002; Thewissen *et al.*, 2006). At the same time Hox genes control the position of both girdles and appendages along the body. In particular, the anterior expression boundaries of HoxC-6 and HoxC-8-10 coincide with the localization of fore- and hindlimb buds respectively (Bejder & Hall, 2002). Reduction and loss of appendages can occur due to regression of

different phases in the conserved genetic pathway for appendage development. Tanaka *et al.* (2005), for example, reported that pelvic-fin loss can be achieved through different mechanisms in pufferfishes and sticklebacks. In the first case, the reduction is due to an altered expression of the gene *Hoxd9a* in lateral mesoderm, whereas in the second case *Pitx1*, a gene responsible for appendage initiation, fails to be expressed (Shapiro *et al.*, 2004). In pythons, limbs development is arrested in two different ways. Forelimb buds are not developed at all, because of the widespread expression of *HoxC-6* and *HoxC-8* genes throughout the lateral plate mesoderm, meaning that no boundary conditions are established for forelimbs to form and therefore there is no pectoral limb initiation (Cohn & Tickle, 1999; Cohn, 2001; Bejder & Hall, 2002). On the contrary, hindlimb buds are formed, but they have a very smooth ectodermal jacket forming a small AER, which causes a precocious interruption of the growth (Cohn, 2001). Serpentine lizards and urodeles have different levels of limb reduction that can vary considerably depending on the species (Greer, 1991). Nevertheless, in general, the formation of their limb buds starts and then regresses, or the expression of *Shh* can have a shortened duration, leading to loss of some digits or of a larger part of the limbs (Raynaud, 1990; Hinchliffe, 2002; Shapiro *et al.*, 2003; Tanaka *et al.*, 2005). As far as cetaceans are concerned, pelvic limb buds begin to form but fail to fully develop, in a similar way to the python hindlimbs (Bejder & Hall, 2002; Tanaka *et al.*, 2005). Nevertheless, it is likely that the mechanism is slightly different from that of snakes, as the dolphin *Stenella attenuata* shows a normal AER during development, but the absence of *Hand2* – one of the upstream regulators of the *Shh* transcription – causes a perturbed initial establishment of the ZPA and the consequent absence of *Shh* expression (Thewissen *et al.*, 2006).

Therefore, fin and limb formation has indeed very conserved genetic and ontogenetic pathways among gnathostomes, but developmental causes of appendage loss can be very diverse within and among different groups (Hall, 2008).

## MATERIAL AND METHODS

We compiled a database (Appendix 1 and 2) that includes 125 species of teleost fishes, 74 species of lissamphibians and 151 species of squamate reptiles. For the taxon sampling of teleost fishes, we selected all the groups characterized by pectoral fin loss: Anguilliformes, Clariidae, Gobionellidae (strong reduction of the pectoral fin in the genus *Luciogobius*), and Trichomycteridae. The groups of Zoarcales and

Mastacembelidae have some finless members, but we did not include them in our analysis, as their ecology and phylogenetic relationship are poorly known.

We combined different phylogenetic trees that contain the group included in the study (either the recent-most or the complete-most phylogenetic analyses), and in particular: Santini *et al.* (2013) for Anguilliformes, Baskin (1973), Datovo & Bockmann (2010), and DoNascimento (2015) for Trichomycteridae, Wright (2017) for Clariidae, and Yamada *et al.* (2009) and Thacker (2013) for Gobionellidae. We sampled part of the taxa contained in these phylogenies, several of them being used as outgroups, as they do not show any pectoral fin loss. Particular attention was paid on groups with finless members included in these phylogenies, among which at least one representative species for every family has been selected, but including all the taxa with complete information about fins and ecological habits that were close to the node where pectoral fins were lost. In fact, for studies concerning causal relationships of specific traits, the most important taxa to sample are the ones near to the node where the trait we want to study (e.g., fin or limb loss) first occurred and got fixed. Any potential evolutionary innovation that originated after the first occurrence and fixation of the trait should not be considered as a potential evolutionary driver and it is therefore not essential to insert many derived taxa in the sample (Macaluso & Tschopp, 2018). The same procedure was followed to compile the database of lissamphibians (complete sample of basal Gymnophiona, Sirenidae, and Amphiumidae), starting from the phylogeny published by Pyron and Wiens (2011), and squamate reptiles (complete sample of basal limbless Agamidae, Amphisbaenia, Anguidae, Anniellidae, Dibamidae, Diploglossidae, Ophidia, Pygopodidae, and Scincidae), using the phylogenies of Reeder *et al.* (2015), Da Silva *et al.* (2018), and Pyron *et al.* (2013).

The taxon sampling was of course limited by the information available for the taxa and we chose species for which the following is known: i) phylogenetic position; ii) presence or absence of appendages; iii) behaviour or ecology. Our limited knowledge of these data is particularly relevant in the case of extinct taxa, because of the difficulty in reconstructing their life habits. Moreover, it is not so common to find a complete articulated skeleton of terrestrial animals that can tell us if appendages were present or not in a certain taxon (see for example the case of the stem-group caecilian described by Evans & Sigogneau-Russell, 2001). For these reasons, the sample of extinct taxa is limited in this study to relatives of extant taxa



representing their stem, whenever information about them is available. We collected information about elongation of the body, presence or absence of the appendages, and lifestyle (see Appendix 1, 2, and 3 for the references). Elongation has only been scored for fishes, which display different kinds of elongation (anguilliform and stiffer-body; Ward & Metha, 2010; Maxwell & Wilson, 2013) and it is therefore important to consider this character in the analysis. In particular, fishes are herein considered as elongated if their length is more than five times the maximum body depth. The considered cases of fin loss in fishes are restricted to those taxa without pectoral fins because the pelvic fins are absent in a huge number of groups due to different factors (e.g., Nelson, 1989). *Luciogobius* has been scored as lacking its pectoral fins as it shows an extreme pectoral fin reduction compared to its close relatives (Hyun-Geun & Seung-Ho, 2014). Squamate reptiles and lissamphibians were scored as lacking their limbs (1) if both pairs of appendages were absent, and as intermediate (01) if only one pair of appendages has been lost. The only exceptions to this rule are snakes with underdeveloped hindlimbs (e.g., pythons, *Pachyrhachis*, *Haasiophis*), the genus *Dibamus* in which the presence of hindlimbs are a sexual dimorphic character (vestigial hindlimbs only present in males; Koppetsch *et al.*, 2019), and *Amphiuma*, which have been scored as limbless although they possess small vestigial hindlimbs useless for locomotion. Lifestyle has been divided in “fossorial” or “not fossorial”. Fishes are scored as 1 concerning “fossoriality” (i.e., column “fossoriality” in Appendix 1) when they have either burrowing habits or are crevices-dwellers, whereas squamate reptiles and lissamphibians were scored as “fossorial” (i.e., 1 in column “fossoriality” in Appendix 2) when they are either burrowers or grass-swimmers. Although burrowing and grass-swimming result in different constraints acting on the whole body, the lateral sides of the body (and consequently the appendages) of burrowing and grass-swimming animals, are constrained in a similar way, by the substrate in burrowers and crevices-dwellers and grass in grass-swimmers. Additional information and references about life style, phylogenetic position, and presence/absence of appendices are present in the supplementary material (Appendix 1, 2, and 3). After collecting these data, we compiled a composite phylogenetic tree in Mesquite (Maddison & Maddison, 2018) reporting all the included taxa, based on already existing phylogenies listed above. We performed the discrete comparative analysis available in the software BayesTraitsV3 (Meade & Pagel, 2017). Discrete comparative analysis is used to test if two binary traits are correlated and its significance is established by

comparing the likelihoods (derived using Markov chain Monte Carlo – MCMC) of two models, one assuming that the traits evolved independently and the other assuming that their evolution is correlated. Two binary traits can be described by four possible states, written as “0,0”, “0,1”, “1,0” and “1,1”. The independent model assumes that the two traits evolve independently, e.g. the transition from 0 to 1 in the first trait is independent from the state of the second trait, whereas the dependent model assumes that the traits are correlated and the rate of change in one trait is dependent from the state of the other. The test was performed structuring an input database as an Excel file of a table at two entrances (see Appendix 1, 2): species in the rows and characters in the columns. Concerning fishes, the two binary characters are pectoral fin loss and a character that is scored as 1 only if the taxon is both elongated (as defined above) with anguilliform locomotion and either fossorial or crevices-dweller. As all the fossorial (or grass-swimmers) lissamphibians and squamates have an extremely elongated body, elongation has not been considered as an essential character in their case and the two binary characters are therefore limb loss and fossoriality or grass-swimming. Given that arbitrary branch lengths are commonly used and well-supported in the literature using Comparative Methods (Grizante *et al.*, 2012, and references therein), we performed the statistical analyses using an arbitrary branch length of 1.0 and all branches were scaled to 0.1, as suggested for the software BayesTraitsV3 (Meade & Pagel, 2017). As is usual in this kind of analysis, we set all the priors to an exponential with a mean of 10 and use the stepping stone sampler with 100 stones and 1000 iterations per stone to estimate the marginal likelihood (see the manual for users of BayesTraitsV3). We performed two different analyses, one for teleost fishes and a separate one for lissamphibians and squamate reptiles, to make it easier to manipulate the large trees in Mesquite. The phylogenetic trees we built are reported in Figures 1 and 2. It is worth noting that in the discrete analysis of BayesTraitsV3 it is not necessary to infer the ancestral state of the characters and thus the coloured branches in the figures are just graphical representations. Here, we evidence the character states with different colours, referring to appendices 1 and 2. In particular, names depicted in red indicate species scored with 1 for appendage loss, whereas light blue species are the ones scored as 01. Colour of the branches refers to the second character, intended as the co-occurrence of eel-like elongation and burrowing behaviour (or crevices or sea-grass inhabitants) for teleost fishes and burrowing or grass-swimming habits for squamate reptiles and lissamphibians.

## RESULTS

The analysis resulted in two values of the marginal likelihood, one for the dependent model and one for the independent model (Table 1). Both are described in a logarithmic scale. To test whether the traits are correlated or not, we calculate a log Bayes Factor between the dependent and independent models. The calculations for Log Bayes factors are given below.

$$\text{Log BF} = 2 (\log \text{marginal likelihood dependent model} - \log \text{marginal likelihood independent model})$$

The Log BF of 41.467358 in one case and of 44.253558 in the other suggest that there is strong evidence for correlated evolution, as a “strong evidence” of correlation is considered when Log BF has values higher than 5 (Gilks *et al.*, 1996).

## DISCUSSION

The environmental conditions may represent relevant evolutionary drivers leading to the emergence of new body morphologies within clades. Nevertheless, very different environmental conditions may provide similar constraints on organisms living – and moving – in them, thereby leading to the development of convergent morphologies. Burrowing (or interstitial) animals, grass-swimmers, and marine crevices-dwellers represent an example of this, because the presence of appendages is not favoured in the environment where they live.

### SQUAMATES AND LISSAMPHIBIANS

Previous hypotheses about squamate reptiles and lissamphibians developing a limbless body plan as an adaptative response to burrowing or grass-swimming (Evans, 1998; Wiens *et al.*, 2006; Da Silva *et al.*, 2018) are confirmed by our results. Basal scolecophidian snakes and more derived fossil taxa (e.g., *Dinilysia*, *Wonambi*) are fossorial (or semifossorial as in the case of *Yurlunggur*; Palci *et al.*, 2018) and several lines of evidence support the hypothesis that the fossoriality of basal snakes is plesiomorphic (Miralles *et al.*, 2018). Moreover, comparative geometric morphometric studies on skulls demonstrated that lizards could not have transitioned to snakes by any other evolutionary path than through fossoriality (Da Silva *et al.*, 2018).

The phylogenetic relationships of the stem lineage of Ophidia are still highly controversial and it is therefore difficult to understand the ecology of the basal-most fossil snakes. For example, the life style of the Cretaceous snake *Coniophis* has been reconstructed as fossorial (Longrich *et al.*, 2012), but its phylogenetic

position is not resolved. In fact, Longrich *et al.* (2012) consider it as the basalmost stem ophidian, but Caldwell *et al.* (2015) place this taxon in a more derived position. The situation is similar as far as most of the stem taxa are concerned. In general, caution is warranted when using single fossil snakes to make broad extrapolations about early snake biology (Palci *et al.*, 2018). It is also still unresolved which one between the body- or head-first hypotheses is the most likely, with different evidence sustaining either the former or the latter (Longrich *et al.*, 2012; Caldwell *et al.*, 2015; Da Silva *et al.*, 2018). It is important, nevertheless, to remark that our results suggest a general evolutionary trend connecting fossoriality (and, more broadly, complex habitats) with limb-loss, but this does not mean that this same evolutionary force acted in every single group that evolved a reduction or loss of the limbs, as different constraints can act in different groups (Macaluso & Tschopp, 2018). There are, in fact, few groups of squamates that evolved a limbless body, which are generalist surface-dwellers. Two remarkable exceptions are, for example, the skinks and the pygopodids. Skinks evolved limblessness independently in several lineages, even within a single genus (e.g., *Lerista*; Skinner *et al.*, 2008; Fig. 3G), many of which are burrowers, whereas some others are also more generalist surface-dwellers (Weins *et al.*, 2006; Camaiti *et al.*, 2019). Pygopodidae is the only family of gekkotans that has members devoid of limbs. They are generally surface-dwellers, even if the basal-most forms live in the litter (Dorrough & Ash, 1999; Wall & Shine, 2013), a lifestyle that can be regarded as fossorial. The fact that limb loss is so common within squamates is not surprising, since elongated reptiles are characterized by an undulatory locomotion and appendages that primarily help to carry forward the body (Sfakiotakis *et al.*, 1999; Grillner, 2011) and limbs can therefore be lost without a relevant impact on their fitness.

Within Amphisbaenia (Fig. 3I), the stem taxon *Slavioia darevskii* apparently proves that fossoriality evolved before the limb loss, as it has clear cranial adaptations for burrowing, but also limbs (Tałanda, 2016). A different phylogenetic analysis placed *Cryptolacerta hassiaca* on the stem of this group (Müller *et al.*, 2011), but the situation is substantially unchanged, as it shows partially reduced limbs and cranial adaptations for burrowing. The same situation is found in the clade Gymnophiona, in which the fossil taxon *Eocaecilia micropodia* possesses fossorial adaptations and small limbs (Jenkins *et al.*, 2007). Salamanders of the family Sirenidae (Fig. 3E) lack hind limbs and show some digital reduction of the

forelimbs and Amphiumidae have very small and motionless limbs, but there is no information on the appendicular skeleton of stem forms referred to these groups (Lande, 1978).

Studies of developmental genetics clearly evidence that there are multiple ways to produce a limbless body plan (Kohlsdorf *et al.*, 2008). In a similar way, it is likely that fin or limb loss in different, unrelated groups may be originated through different evolutionary drivers. In any case, our analysis suggests that there is a general correlation between burrowing or grass-swimming habits and limb loss.

## TELEOSTS

As far as fishes are concerned, the situation is more complex, because of their locomotion style. Fishes generally use the caudal fin as a propulsor, whereas the paired fins are used to control lateral movement and to prevent rolling and pitching, although there are also fishes that use oscillatory or undulatory movements of the paired fins as thrust generation (see Sfakiotakis *et al.*, 1999 for an extensive review on fish swimming mode). Short-bodied fishes with ostraciiform swimming mode as well as elongated fishes with carangiform locomotion use their pectoral (and pelvic) fins to control their body and therefore they simply cannot lose their fins, even if this change would be advantageous in their environment. On the contrary, the anguilliform swimming mode may permit the loss of paired fins without a remarkable effect on locomotion capability. In this case, in fact, the paired fins are not useful to prevent rolling or pitching, even if they can help locomotion (Sfakiotakis *et al.*, 1999). This is also clearly demonstrated by the cetaceans and sirenians, the only mammal clades with representatives characterized by elongated bodies, which lose a pair of appendages. During the course of their evolutionary history, cetaceans and sirenians have lost pelvic fins, in a similar way to numerous fish clades (e.g., Nelson, 1989, Bejder & Hall, 2002). Their locomotion is undulatory, but differently from that of eel-like fishes, since waves are produced in a vertical plane, which do not prevent from the rolling and pitching problems. This is surely coupled with the fact that they did not lose their pectoral fins, which have acquired a stabilizing and steering function, not generating any propulsive movements (Bejder & Hall, 2002). Our results show that fin loss in fishes is restricted to taxa characterized by an eel-like morphology of the body and most likely related to the burrowing lifestyle or to cryptic life in reef ecosystems. This is clearly evidenced by the consistently eel-like morphology of finless taxa that are characterized by burrowing or crevice-dwelling habits (e.g., Muraenidae; Fig. 3A). The most diverse clade of

eel-like fishes is the elopomorph order Anguilliformes, in which pelvic fins are generally absent, but pectoral fins are present in some groups. Although the interpretation of the ecological preference of extinct fishes is not always easy, it is reasonable to hypothesize that basal anguilliforms (e.g., *Anguillavus* or *Luenchelys*; Belouze, 2002; Belouze *et al.*, 2003 a,b) were in some ways reef-associated, because the Cretaceous plattenkalk deposits in which they have been found originated on the outer part of the Lebanese carbonate platform, which was mostly occupied by oyster and rudist mounds and patch reefs (Hemleben & Swimburne, 1991). Members of the extant families Protanguillidae and Synphobranchidae, regarded as the most basal lineages of crown Anguilliformes (Santini *et al.*, 2013), have small pectoral fins, and are characterized by a variety of ecological adaptations. For example, protoanguillids live in submarine caves (Johnson *et al.*, 2011) and the most basal synphobranchid, *Simenchelys parasitica*, developed a peculiar parasitic lifestyle (e.g., Jaquet, 1920). The main anguilliform group of real burrowers is the Moringuidae, whose members are in general burrowers (head or tail-first) or crevice-dwellers with a marked reduction of paired fins (Castle, 1986; Allen & Steene, 1988; De Schepper *et al.*, 2005). The extant species of the genus *Anguilla* are demersal and do not show a clear reduction of the paired fins, a pattern also shared with three extinct species, *A. ignota*, *A. multiradiata* and *A. elegans* (Winckler, 1861; Micklich, 1985; Riede, 2004; Gaudant *et al.*, 2018). Some lineages within the family Congridae (i.e. the clade composed by *Ariosoma*, *Heteroconger* and *Paraconger*, see Santini *et al.*, 2013) includes burrowing fishes devoid of paired fins (Smith, 1981; Riede, 2004; Bacchet *et al.*, 2006). Pectoral fins are lost also in certain crevices-dwelling species belonging to the family Muraenidae (Robins *et al.*, 1991; Chen *et al.*, 1994; Lieske & Myers, 1994; McCosker, 2010; Reece *et al.*, 2010).

A unique case is the benthic gobionellid genus *Luciogobius*, because it is probably the only fish taxon adapted to an interstitial life in gravel beaches (Yamada *et al.*, 2009). The main adaptation consists in an anguilliform elongation of the body that confer it enough agility to move in a three-dimensional complex habitat, similar to that characteristic of terrestrial and aquatic burrowers (Gans, 1975; Yamada *et al.*, 2009). Interestingly, in parallel with the elongation of the body, interstitial species of *Luciogobius* (Fig. 3C) underwent fin reduction, whereas elongated species of Gobionellidae, which are not interstitial but have a benthic or nektonic lifestyle (e.g., genera *Inu* or *Clariger*), exhibit completely developed paired fins. A

similar condition is also characteristic of those species of the Gobionellidae that live in reefs or on muddy substrates but are not eel-shaped (e.g., *Periophtalmus barbarous*, *Scartelaos histiophorus*).

Within the Neotropical catfish family Trichomycteridae, the Glanapteryginae are interstitial fishes living in complex habitats and they are mostly eel-shaped with a clear reduction of paired fins, which are usually very thin becoming filiform and without any equilibrium function (De Pinna, 1988; Schaefer *et al.*, 2005; Villa-Verde & Costa, 2006). Catfishes belonging to Clariidae are generally elongated, with an anguilliform swimming mode that is often limited to the posterior part of the body, also extending to its anterior part in some species. All the species devoid of paired fins live in complex or highly vegetated habitats, thereby confirming the hypothesis of fin reduction driven by environmental complexity (Fig. 3B; see Appendix 1 for references).

Finally, the Mastacembelidae represent another very peculiar case, as they are eel-shaped fishes, also called spiny eels because of the long series of dorsal-fin spines (Vreven, 2005). It is worth mentioning them because of the particular case of the only two species of this group (*Mastacembelus apectoralis* (Fig. 3D) and its sister taxon, *M. micropectus*) that exhibit a considerable reduction in pectoral-fin size, which is considered to be related to the highly structured environments they live in (Brown *et al.*, 2011). Their phylogenetic relationships are poorly known, and thus they have not been sampled in our comparative analysis.

Our study reveals the existence of a correlation between the reduction and/or loss of pectoral fins and the coexistence of an eel-like body morphology, which makes unnecessary the use of pectoral fins to prevent rolling and pitching, and of an environmental constraint due to burrowing and crevice- or seagrass-dwelling. In fact, whereas being different habitat, the latter all have a similar effect on the appendages of fishes, because paired fins may hamper a free movement in these constrained environments. A similar correlation between burrowing or grass-swimming habits and limb loss is found also in squamate reptiles and lissamphibians, but the structural constraints are much less important in these groups as the locomotion is less constrained by appendages than in fishes due to the absence of balance problems.

## FUTURE PERSPECTIVES

A relation between long-tailed patterns and surface dwelling, and conversely pre-caudally elongated morphotypes and burrowers has been proposed for squamates reptiles (Bellairs & Underwood, 1951; Evans, 1998), even if this hypothesis has never been proved with rigorous analyses. An interesting future perspective is to expand this hypothesis to anguilliform fishes. In fact, crevice- and seagrass-dwellers could be somehow associated with terrestrial surface-dwellers. Mehta *et al.* (2010) reported that the elongation in muraenids (i.e., crevices-dwellers) results from the addition of caudal rather than precaudal vertebrae to their axial skeleton, whereas elongation of the body in ophichthids and congrid (i.e. burrowers) is achieved by adding a similar number of vertebrae to their precaudal and caudal regions; however, additional studies on this subject including a larger taxon sampling and much more comparative information would be desirable.

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## Figure and tables captions

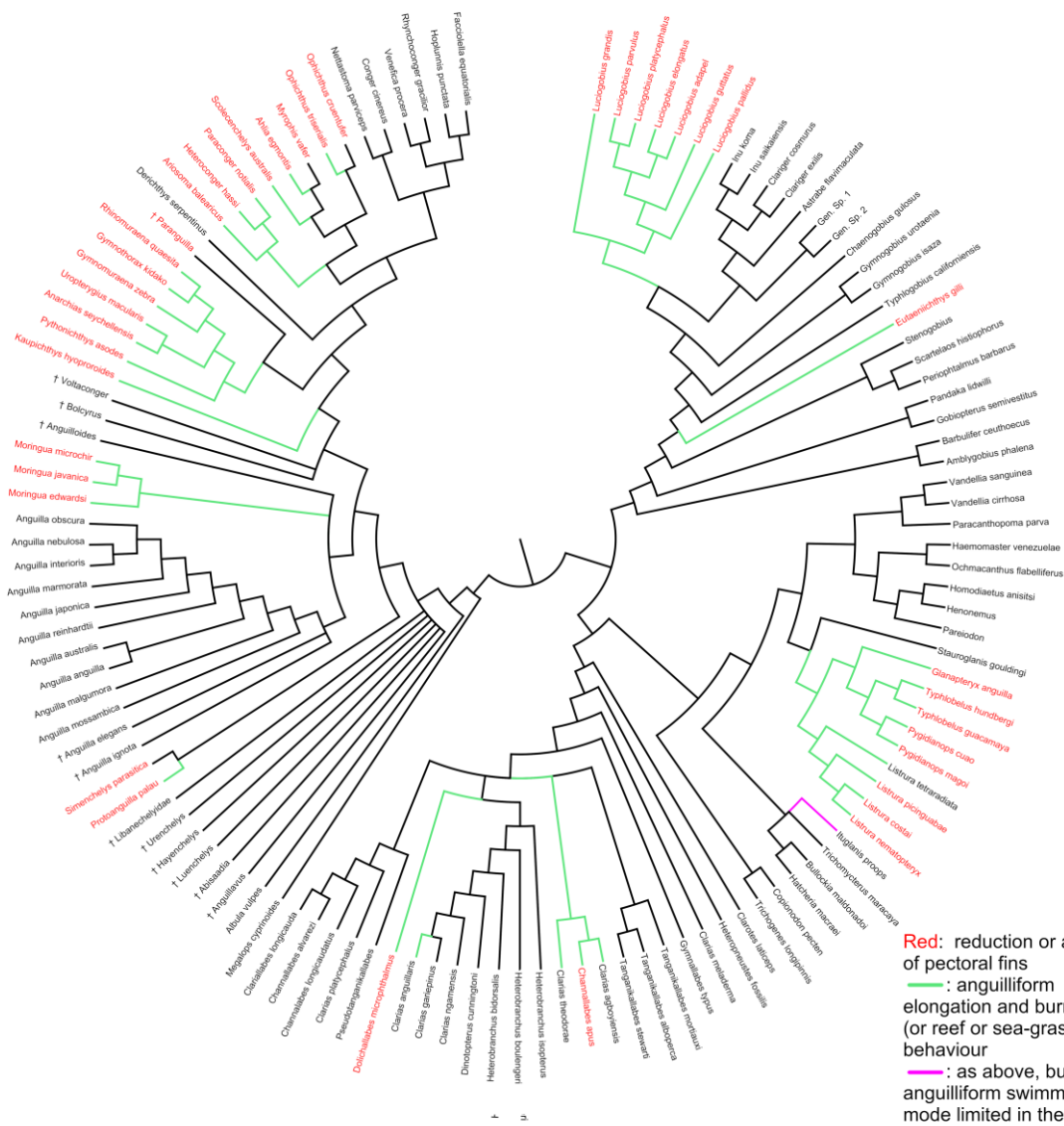
**Figure 1.** Composite phylogenetic tree of teleost fishes used for the analysis. See material and methods for the references concerning phylogenetic position and character state reconstruction. The coloured branches in the figure are just graphical representations and they do not represent any ancestral state reconstruction, as it is not a necessary step for the discrete comparative analysis using BayesTraitsV3.

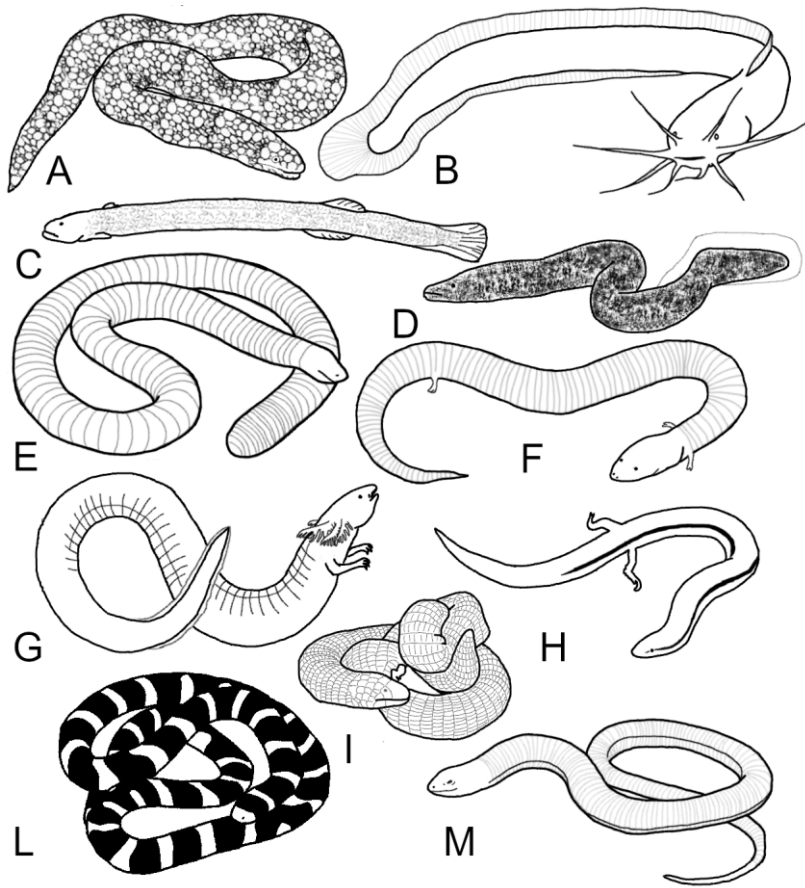
**Figure 2.** Composite phylogenetic tree of lissamphibians and squamates used for the analysis. See material and methods for the references concerning phylogenetic position and character state reconstruction. The coloured branches in the figure are just graphical representations and they do not represent any ancestral state reconstruction, as it is not a necessary step for the discrete comparative analysis using BayesTraitsV3.

**Figure 3.** Examples of elongated vertebrate with fin or limb reduction or loss. A, *Anarchias seychellensis*, crevice-dweller (fish); B, *Channalabes apus*, living among tree roots (fish); C, *Luciogobius elongatus*, interstitial (fish); D, *Mastacembelus apectoralis*, living among sea vegetation (fish); E, *Caecilia volcani*, burrower (amphibian); F, *Amphiuma means*, burrower (amphibian); G, *Siren lacertina*, burrower (amphibian); H, *Lerista bipes*, surface-dweller (reptile); I, *Blanus cinereus*, burrower (reptile); L, *Anilius scytale*, burrower (reptile); M, *Pseudopus apodus*, grass-swimmer (reptile).

**Table 1.** Values of Log of marginal likelihood of the dependent and independent models, and Bayes Factor (BF) obtained using BayesTraitsV3. In both teleost fishes and lissamphibians and reptiles the logarithmic values of the Bayes Factor indicate a strong evidence of correlation.







**Appendix 1.** Teleost fishes database. Grey columns are the two columns used for the discrete analysis.

Taxon	Group	Elongation	Anguilli form locomotion	Pectoral fins absent	Fossorial/complex habitat	Notes	Anguilli form + fossoriality	Data's reference	Phylogeny's reference
<i>Megalops cyprinoides</i>	Elopomorph a	0	0	0	0	reef-associated	0	Riede, 2004	Santini <i>et al.</i> , 2013
<i>Albula vulpes</i>	Elopomorph a	0	0	0	0	reef-associated	0	Riede, 2004	Santini <i>et al.</i> , 2013
† <i>Anguillavus</i>	Elopomorph a	1	1	0	0	reef	0	Belouze, 2002	Pfaff <i>et al.</i> , 2016
† <i>Abisaadia</i>	Elopomorph a	1	1	0	0	reef	0	Belouze <i>et al.</i> , 2003 a	Pfaff <i>et al.</i> , 2016
† <i>Luenchelys</i>	Elopomorph a	1	1	0	0	reef	0	Belouze <i>et al.</i> , 2003 b	Pfaff <i>et al.</i> , 2016
† <i>Hayenchelys</i>	Elopomorph a	1	1	0	0	reef	0	Belouze <i>et al.</i> , 2003 a	Pfaff <i>et al.</i> , 2016
† <i>Urenchelys</i>	Elopomorph a	1	1	0	0	reef	0	Belouze, 2002	Pfaff <i>et al.</i> , 2016
† <i>Libanechelyidae</i>	Elopomorph a	1	1	0	0	reef	0	Taverne, 2004	Pfaff <i>et al.</i> , 2016

<i>Protoanguilla palau</i>	Anguilliformes	1	1	01	1	cave, reef associated	1	Belouze <i>et al.</i> , 2003 a	Santini <i>et al.</i> , 2013
<i>Simenchelys parasitica</i>	Synaphobranchidae Anguilliformes	1	1	1	0	parasitic	0	Shcherbachev, 1997	Santini <i>et al.</i> , 2013 Pfaff <i>et al.</i> , 2016
† <i>Anguilloides</i>		1	1	0	0	reef burrower, head-first; small, vestigial	0	Blot, 1984	
<i>Moringua edwardsi</i>	Moringuidae	1	1	1	1	pectoral fins burrower in sand; small, vestigial	1	Smith, 1997	Santini <i>et al.</i> , 2013
<i>Moringua microchir</i>	Moringuidae	1	1	1	1	pectoral fins	1	Castle, 1986 Allen & Steene, 1988	Santini <i>et al.</i> , 2013
<i>Moringua javanica</i>	Moringuidae	1	1	1	1	reef	1		Santini <i>et al.</i> , 2013
† <i>Anguilla ignota</i>	Anguillidae	1	1	0	0	freshwater	0	Micklich, 1985	Pfaff <i>et al.</i> , 2016
† <i>Anguilla multiradiata</i>	Anguillidae	1	1	0	0	freshwater	0	Micklich, 1985	Pfaff <i>et al.</i> , 2016
† <i>Anguilla elegans</i>	Anguillidae	1	1	0	0	freshwater	0	Winckler, 1861	Pfaff <i>et al.</i> , 2016
<i>Anguilla mossambica</i>	Anguillidae	1	1	0	0	demersal	0	Riede, 2004	Santini <i>et al.</i> , 2013
<i>Anguilla malgumora</i>	Anguillidae	1	1	0	0	under rocks in flowstreams	0	Martin-Smith & Tan, 1998	Santini <i>et al.</i> , 2013
<i>Anguilla anguilla</i>	Anguillidae	1	1	0	0	demersal	0	Riede, 2004 McDowall & Beumer, 1980	Santini <i>et al.</i> , 2013
<i>Anguilla australis</i>	Anguillidae	1	1	0	0	demersal	0		Santini <i>et al.</i> , 2013
<i>Anguilla reinhardtii</i>	Anguillidae	1	1	0	0	demersal	0	Riede, 2004	Santini <i>et al.</i> , 2013
<i>Anguilla japonica</i>	Anguillidae	1	1	0	0	demersal	0	Yamada <i>et al.</i> , 1995	Santini <i>et al.</i> , 2013
<i>Anguilla marmorata</i>	Anguillidae	1	1	0	0	demersal	0	Rainboth, 1996	Santini <i>et al.</i> , 2013
<i>Anguilla</i>	Anguillidae	1	1	0	0	demersal	0	Allen <i>et al.</i>	Santini <i>et al.</i>

<i>obscura</i>					al		<i>al.</i> , 2002	<i>al.</i> , 2013
<i>Anguilla</i>					demers		Riede,	Santini <i>et</i>
<i>interioris</i>	Anguillidae	1	1	0	0 al	0	2004	<i>al.</i> , 2013
<i>Anguilla</i>					demers		Riede,	Santini <i>et</i>
<i>nebulosa</i>	Anguillidae	1	1	0	0 al	0	2004	<i>al.</i> , 2013
							Pfaff <i>et</i>	
† <i>Voltaconger</i>	Congroidea	1	1	0	0 ?	0	Blot, 1984	<i>al.</i> , 2016
							Pfaff <i>et</i>	
† <i>Bolcyrus</i>	Congroidea	1	1	0	0 ?	0	Blot, 1984	<i>al.</i> , 2016
<i>Derichthys</i>	Derichthyda				mesope		Mundy,	Santini <i>et</i>
<i>serpentinus</i>	e	1	1	0	0 lagic	0	2005	<i>al.</i> , 2013
<i>Nettastoma</i>							Smith <i>et</i>	Santini <i>et</i>
<i>parviceps</i>	Congridae	1	1	0	0 abissale	0	<i>al.</i> , 1981	<i>al.</i> , 2013
<i>Conger</i>							Myers,	Santini <i>et</i>
<i>cinereus</i>	Congridae	1	1	0	0 reef	0	1991	<i>al.</i> , 2013
							McEachra	
							n &	
<i>Venefica</i>							Fechhelm,	Santini <i>et</i>
<i>procera</i>	Congridae	1	1	0	0 abissale	0	1998	<i>al.</i> , 2013
<i>Rhynchoconge</i>							Robins &	Santini <i>et</i>
<i>r gracilior</i>	Congridae	1	1	0	0 abissale	0	Ray, 1986	<i>al.</i> , 2013
<i>Facciolella</i>							Love <i>et</i>	Santini <i>et</i>
<i>equatorialis</i>	Congridae	1	1	0	0 abissale	0	<i>al.</i> , 2005	<i>al.</i> , 2013
<i>Hoplunnis</i>							Smith,	Santini <i>et</i>
<i>punctata</i>	Congridae	1	1	0	0 abissale	0	1990	<i>al.</i> , 2013
<i>Ariosoma</i>					burrow		Riede,	Santini <i>et</i>
<i>balearicus</i>	Congridae	1	1	01	1 er, reef	1	2004	<i>al.</i> , 2013
<i>Heteroconger</i>					burrow		Bacchet <i>et</i>	Santini <i>et</i>
<i>hassi</i>	Congridae	1	1	1	1 er, reef	1	<i>al.</i> , 2006	<i>al.</i> , 2013
					burrow			
<i>Paraconger</i>					er, tail-		Smith,	Santini <i>et</i>
<i>notialis</i>	Congridae	1	1	01	1 first	1	1981	<i>al.</i> , 2013
							Hibino &	
<i>Scolecenchelys</i>	Ophichthida				seagras		Kimura,	Santini <i>et</i>
<i>australis</i>	e	1	1	1	1 s	1	2015	<i>al.</i> , 2013
					seagras			
	Ophichthida				s and		Robins &	Santini <i>et</i>
<i>Ahlia egmontis</i>	e	1	1	1	1 crevices	1	Ray, 1986	<i>al.</i> , 2013
					benthic			
	Ophichthida				but not		Charter &	Santini <i>et</i>
<i>Myrophis vafer</i>	e	1	1	01	0 er	0	Moser,	<i>al.</i> , 2013
							McCosker	
					burrow		&	
<i>Ophichthus</i>	Ophichthida				1 er	1	Rosenblatt	Santini <i>et</i>
<i>triserialis</i>	e	1	1	01	0 offshor	0	, 1998	<i>al.</i> , 2013
<i>Ophichthus</i>	Ophichthida				0 e water	0	Robins &	Santini <i>et</i>
<i>cruentifer</i>	e	1	1	01			Ray, 1986	<i>al.</i> , 2013
<i>Kaupichthys</i>	Anguillifor						Claro,	Santini <i>et</i>
<i>hyoproroides</i>	mes	1	1	01	0 reef	01	1994	<i>al.</i> , 2013
	Anguillifor						Pfaff <i>et</i>	
† <i>Paranguilla</i>	mes	1	1	01	0 reef	0	Blot, 1984	<i>al.</i> , 2016
<i>Pythonichthys</i>	Heterencheli				burrow		Rosenblatt	Santini <i>et</i>
<i>asodes</i>	dae	1	1	1	1 er in	1	&	<i>al.</i> , 2013

					mud		Rubinoff, 1972	
<i>Anarchias seychellensis</i>	Muraenidae	1	1	1	1 crevices	1	Reece <i>et al.</i> , 2010	Santini <i>et al.</i> , 2013
<i>Uropterygius macularis</i>	Muraenidae	1	1	1	1 crevices	1	Robins <i>et al.</i> , 1991	Santini <i>et al.</i> , 2013
<i>Gymnomuraena zebra</i>	Muraenidae	1	1	1	1 crevices	1	Lieske & Myers, 1994	Santini <i>et al.</i> , 2013
<i>Gymnothorax kidako</i>	Muraenidae	1	1	1	1 crevices	1	Chen <i>et al.</i> , 1994	Santini <i>et al.</i> , 2013
<i>Rhinomuraena quaesita</i>	Muraenidae	1	1	1	1 crevices burrow er, interstit ial, small pectoral fins	1	McCosker , 2010	Santini <i>et al.</i> , 2013
<i>Luciogobius elongatus</i>	Gobionellida e	1	1	01	1 burrow er, interstit ial, small pectoral fins	1	Hyun-Geun & Seung-Ho, 2014; Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
<i>Luciogobius adapel</i>	Gobionellida e	1	1	01	1 burrow er, interstit ial, small pectoral fins	1	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
<i>Luciogobius parvulus</i>	Gobionellida e	1	1	01	1 burrow er, interstit ial, small pectoral fins	1	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
<i>Luciogobius platycephalus</i>	Gobionellida e	1	1	01	1 burrow er, interstit ial, small pectoral fins	1	Hyun-Geun & Seung-Ho, 2014; Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
<i>Luciogobius guttatus</i>	Gobionellida e	1	1	01	1 burrow er, small pectoral fins	1	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
<i>Luciogobius pallidus</i>	Gobionellida e	1	1	01	1 burrow er, small pectoral fins	1	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
<i>Luciogobius grandis</i>	Gobionellida e	1	1	01	1 small	1	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009

					pectoral fins			
					intertid al rocky			
<i>Inu koma</i>	Gobionellida e	1	1	0	0 shore	0	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
					intertid al rocky			
<i>Inu saikaiensis</i>	Gobionellida e	1	1	0	0 shore	0	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
					intertid al rocky			
<i>Gen. Sp. 1</i>	Gobionellida e	1	1	0	0 shore,	0	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
					intertid al rocky			
<i>Gen. Sp. 2</i>	Gobionellida e	1	1	0	0 shore,	0	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
					subtidal			
<i>Clariger cosmurus</i>	Gobionellida e	1	1	0	0 rocky	0	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
					shore			
					subtidal			
<i>Clariger exilis</i>	Gobionellida e	1	1	0	0 rocky	0	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
					shore			
<i>Astrabe flavimaculata</i>	Gobionellida e	0	0	0	0 subtidal	0	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
					rocky			
<i>Chaenogobius gulosus</i>	Gobionellida e	0	0	0	0 shore	0	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
<i>Gymnogobius isaza</i>	Gobionellida e	0	0	0	0 freshwa	0	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
<i>Gymnogobius urotaenia</i>	Gobionellida e	0	0	0	0 ter lake	0	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
					freshwa			
					ter lake			
<i>Typhlogobius californiensis</i>	Gobionellida e	0	0	0	0 mudshri	0	Yamada <i>et al.</i> , 2009	Yamada <i>et al.</i> , 2009
					mp			
					burrow			
<i>Eutaeniichthys gilli</i>	Gobionellida e	1	1	1	1 mp	1	Henmi & Itani, 2014	Henmi & Itani, 2014
					burrow			
<i>Stenogobius</i>	Gobionellida e	0	0	0	0 er	0	Watson, 1991	Thacker, 2013
<i>Periophtalmus barbarus</i>	Gobionellida e	1	0	0	1 reef,	0	Miller, 1981	Thacker, 2013
					amphibi			
					ous			
<i>Scartelaos histiophorus</i>	Gobionellida e	1	0	0	1 mud,	0	Riede, 2004	Thacker, 2013
					amphibi			
<i>Gobiopterus semivestitus</i>	Gobionellida e	0	0	0	0 ous	0	Thacker, 2013	Thacker, 2013
<i>Pandaka lidwilli</i>	Gobionellida e	0	0	0	0	0	Masuda <i>et al.</i> , 1984	Thacker, 2013
<i>Barbulifer ceut hoecus</i>	Gobiidae	0	0	0	1 pelagic	0	Cervigón, 1994	Thacker, 2013
<i>Amblygobius phalena</i>	Gobiidae	0	0	0	1 reef	0	Randall, 1995	Thacker, 2013
<i>Copionodon</i>	Copionodont	1	0	0	0	0	Zanata &	Datovo &



<i>pecten</i>	inae							Primitivo, 2014	Lindam, 2005
<i>Trichogenes longipinnis</i>	Trichogeninae	1	0	0	0			0 Britski & Ortega, 1982; Sazima, 2004	Datovo & Lindam, 2005
<i>Bullockia maldonadoi</i>	Trichomycterinae	1	0	0	0			0 Bockman & Sazima, 2004	Datovo & Lindam, 2005
<i>Hatcheria macraei</i>	Trichomycterinae	1	0	0	0			0 Bockman & Sazima, 2004	Datovo & Lindam, 2005
<i>Ituglanis proops</i>	Trichomycterinae	1	1	0	0			01 Bockman & Sazima, 2004	Datovo & Lindam, 2005
<i>Trichomycterus maracaya</i>	Trichomycterinae	1	0	0	0			0 Bockman & Sazima, 2004	Datovo & Lindam, 2005
<i>Listrura tetraradiata</i>	Glanapteryginae	1	1	0	1	interstitial		1 Villa-Verde & Costa, 2006	Baskin, 1973; Datovo & Lindam, 2005; Villa-Verde <i>et al.</i> , 2012
<i>Listrura picinguabae</i>	Glanapteryginae	1	1	1	1	interstitial, filiform fins		1 Villa-Verde & Costa, 2006	Baskin, 1973; Datovo & Lindam, 2005; Villa-Verde <i>et al.</i> , 2012
<i>Listrura nematopteryx</i>	Glanapteryginae	1	1	1	1	interstitial, filiform fins		1 De Pinna, 1988; Villa-Verde & Costa, 2006	Baskin, 1973; Datovo & Lindam, 2005; Villa-Verde <i>et al.</i> , 2012
<i>Listrura costai</i>	Glanapteryginae	1	1	1	1	interstitial, filiform fins		1 Villa-Verde & Costa, 2006; Villa-Verde <i>et al.</i> , 2012	Baskin, 1973; Datovo & Lindam, 2005; Villa-Verde <i>et al.</i> , 2012

<i>Glanapteryx anguilla</i>	Glanapteryginae	1	1	1	1	leaf litter	1	De Pinna, 1988; Schaefer <i>et al.</i> , 2005	Baskin, 1973; Datovo & Lindam, 2005
<i>Pygidianops cuao</i>	Glanapteryginae	1	1	1	1	small, filiform pectoral fins	1	Schaefer <i>et al.</i> , 2005	Baskin, 1973; Datovo & Lindam, 2005
<i>Pygidianops magoi</i>	Glanapteryginae	1	1	1	1	sand-bottom	1	Schaefer <i>et al.</i> , 2005	Baskin, 1973; Datovo & Lindam, 2005
<i>Typhlobelus hundbergi</i>	Glanapteryginae	1	1	1	1	sand-bottom	1	Schaefer <i>et al.</i> , 2005	Baskin, 1973; Datovo & Lindam, 2005
<i>Typhlobelus guacamaya</i>	Glanapteryginae	1	1	1	1	sand-bottom	1	Schaefer <i>et al.</i> , 2005	Baskin, 1973; Datovo & Lindam, 2005
<i>Stauroglanis gouldingi</i>	Sarcoglanidinae	0	0	0	0	rheophilic	0	Zuanon & Sazima, 2004; Schmidt, 1993;	Baskin, 1973; Datovo & Lindam, 2005
<i>Paracanthopoma parva</i>	Vandelliinae	1	1	0	0	parasitic	0	Zuanon & Sazima, 2005	Baskin, 1973; DoNascimento, 2015
<i>Vandellia sanguinea</i>	Vandelliinae	1	1	0	0	blood parasit	0	Baskin <i>et al.</i> , 1980	Baskin, 1973; DoNascimento, 2015
<i>Vandellia cirrhosa</i>	Vandelliinae	1	1	0	0	blood parasit	0	Baskin <i>et al.</i> , 1980	Baskin, 1973; DoNascimento, 2015
<i>Haemomaster venezuelae</i>	Stegophilinae	1	1	0	0	parasitic	0	DoNascimento, 2015	DoNascimento, 2015
<i>Ochmacanthus flabelliferus</i>	Stegophilinae	1	1	0	0	parasitic	0	DoNascimento, 2015	DoNascimento, 2015

<i>Homodiaetus anisitsi</i>	Stegophilinae	1	1	0	0	parasitic	0	DoNascimento, 2015	DoNascimento, 2015
<i>Henonemus</i>	Stegophilinae	1	1	0	0	parasitic	0	DoNascimento, 2015	DoNascimento, 2015
<i>Pareiodon Clarotes laticeps</i>	Stegophilinae	1	1	0	0	parasitic	0	DoNascimento, 2015	DoNascimento, 2015
<i>Heteropneustes fossilis</i>	Siluroidea	0	0	0	0		0	Risch, 2003	Wright, 2017
<i>Clarias meladerma</i>	Siluroidea	1	0	0	0		0	Ali <i>et al.</i> , 2015	Wright, 2017
	Clariidae	1	01	0	0		0	Vidthayanon, 2002	Wright, 2017
<i>Gymnallabes typus</i>	Clariidae	1	1	0	0		0	Teugels, 2003;	
<i>Tanganikallabes mortiauxi</i>	Clariidae	1	1	0	0		0	Ward <i>et al.</i> , 2015	Wright, 2017
<i>Tanganikallabes alboperca</i>	Clariidae	1	1	0	0		0	Seegers, 2008	Wright, 2017
<i>Tanganikallabes stewarti</i>	Clariidae	1	1	0	0		0	Seegers, 2008	Wright, 2017
<i>Channallabes apus</i>	Clariidae	1	1	1	1	among trees roots, testa piccola rispetto agli altri	1	Seegers, 2008	Wright, 2017
<i>Clarias agboyiensis</i>	Clariidae	1	1	0	1	grasslands shallow s in vegetated areas high variability in fins, but often very small	1	Ezenwaji & Inyang, 1998	Wright, 2017
<i>Clarias theodora</i>	Clariidae	1	1	0	1		1	Teugels, 1986	Wright, 2017
<i>Dolichallabes microphthalmus</i>	Clariidae	1	1	1	1		1	Devaere <i>et al.</i> , 2004;	Wright, 2017
<i>Heterobranchius isopterus</i>	Clariidae	1	01	0	0		0	Seegers, 2008	Wright, 2017
<i>Heterobranchius boulengeri</i>	Clariidae	1	01	0	0		0	Teugels <i>et al.</i> , 1990	Wright, 2017
<i>Heterobranchius bidorsalis</i>	Clariidae	1	01	0	0		0	Teugels <i>et al.</i> , 1990	Wright, 2017
<i>Dinotopterus</i>	Clariidae	1	01	0	0	on	0	Poll, 1953	Wright,

<i>cunningtoni</i>						rocky substrat es perman ent		2017	
<i>Clarias ngamensis</i>	Clariidae	1	1	0	0	swamps	0	Teugels, 1986	Wright, 2017
<i>Clarias anguillaris</i>	Clariidae	1	1	0	1	er	1	Teugels, 1986	Wright, 2017
<i>Clarias gariiepinus</i>	Clariidae	1	1	0	0	rivers	0	Teugels, 1986	Wright, 2017
<i>Pseudotangani kallabes</i>	Clariidae	1	01	0	0		0	Wright, 2017	Wright, 2017
<i>Clarias platycephalus</i>	Clariidae	1	1	0	0		0	Teugels, 1986	Wright, 2017
<i>Channallabes longicaudatus</i>	Clariidae	1	1	0	0		0	Devaere <i>et al.</i> , 2007	Wright, 2017
<i>Channallabes alvarezi</i>	Clariidae	1	1	0	0		0	Devaere <i>et al.</i> , 2007	Wright, 2017
<i>Clariallabes longicauda</i>	Clariidae	1	1	0	0		0	Teugels, 1986	Wright, 2017

**Appendix 2.** Database of squamate reptiles and lissamphibians. Grey columns are the two columns used for the discrete analysis.

Taxon	Group	Absen ce foreli mb	Absen ce hindli mb	Absen ce limb	Burrow ing or grass- swimme r	Notes	Data's reference	Phylogeny's reference
<i>Anelytropsis papillosus</i>	Squamata, Dibamidae	1	1	1	1	burrower	IUCN Red List; Vitt & Caldwell, 2009; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Dibamus novaeguineae</i>	Squamata, Dibamidae	1	1	1	1	burrower	IUCN Red List; Vitt & Caldwell, 2009; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Nephrurus vertebralis</i>	Gekkota, Carphodactyli dae	0	0	0	0	wood	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Underwoodis aurus seorsus</i>	Gekkota, Carphodactyli dae	0	0	0	0	rocky areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Lialis burtonis</i>	Gekkota, Pygopodidae	1	1	1	0	litter	IUCN Red List; Vitt & Caldwell, 2009; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Delma labialis</i>	Gekkota, Pygopodidae	1	1	1	0	litter	IUCN Red List; Vitt & Caldwell, 2009; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015

<i>Pygopus nigriceps</i>	Gekkota, Pygopodidae	1	1	1	0	generalist generalist (burrowing, according to IUCN Red List)	2009; Uetz <i>et al.</i> , 2019 IUCN Red List; Vitt & Caldwell, 2009; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Aprasia aurita</i>	Gekkota, Pygopodidae	1	1	1	0		IUCN Red List; Vitt & Caldwell, 2009; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Rhacodactylus leachianus</i>	Gekkota, Diplodactylidae	0	0	0	0	arboreal	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Coleonyx variegatus</i>	Gekkota, Eublepharidae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Eublepharis hardwickii</i>	Gekkota, Eublepharidae	0	0	0	0	wood	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Hemitheconyx caudicinctus</i>	Gekkota, Eublepharidae	0	0	0	0	savannah	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Hemidactylus turcicus</i>	Gekkota, Gekkonidae	0	0	0	0	generalist	IUCN Red List; Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Mediodactylus kotschy</i>	Gekkota, Gekkonidae	0	0	0	0	rocky areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Phelsuma lineata</i>	Gekkota, Gekkonidae	0	0	0	0	arboreal	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Gonatodes albogularis</i>	Gekkota, Sphaerodactylidae	0	0	0	0	arboreal, generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Euleptes europaea</i>	Gekkota, Sphaerodactylidae	0	0	0	0	rocky areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Pristurus rupestris</i>	Gekkota, Sphaerodactylidae	0	0	0	0	rocky areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Sphaerodactylus schwartzi</i>	Gekkota, Sphaerodactylidae	0	0	0	0	litter	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015

	dae						<i>et al.</i> , 2019	
<i>Asaccus platyrhynchus</i>	Gekkota, Phyllodactylidae	0	0	0	0	rocky areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Tarentola mauritanica</i>	Gekkota, Phyllodactylidae	0	0	0	0	rocky areas	IUCN Red List; Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Phyllodactylus reissii</i>	Gekkota, Phyllodactylidae	0	0	0	0	arid areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>† Ardeosaurus brevipes</i>	Scincoidea	0	0	0	0	generalist	Talanda, 2018	Talanda, 2018
<i>† Yabeinosaurus robustus</i>	Scincoidea	0	0	0	0	generalist	Talanda, 2018	Talanda, 2018
<i>Acontias meleagris</i>	Squamata, Scincidae, Acontinae	1	1	1	1	burrowing	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Acontias gariensis</i>	Squamata, Scincidae, Acontinae	1	1	1	-	?	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Acontias lineatus</i>	Squamata, Scincidae, Acontinae	1	1	1	-	?	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Typhlosaurus braini</i>	Squamata, Scincidae, Acontinae	1	1	1	1	burrowing	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Typhlosaurus caecus</i>	Squamata, Scincidae, Acontinae	1	1	1	1	burrowing	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Typhlosaurus lomiae</i>	Squamata, Scincidae, Acontinae	1	1	1	1	burrowing	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Egernia kingii</i>	Squamata, Scincidae, Egerniinae	0	0	0	0	rocky areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Tiliqua scincoides</i>	Squamata, Scincidae, Egerniinae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Cyclodomorphus michaeli</i>	Squamata, Scincidae, Egerniinae	0	0	0	0	coastal environment	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Liopholis whitii</i>	Squamata, Scincidae, Egerniinae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Ablepharus kitaibelii</i>	Squamata, Scincidae, Eugongylinae	0	0	0	0	arid areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Ablepharus budaki</i>	Squamata, Scincidae, Eugongylinae	0	0	0	0	litter	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015

<i>Feylinia currori</i>	Squamata, Scincidae, Scincinae	1	1	1	01	semi fossorial	IUCN Red List; Wagner & Schmitz, 2006; Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Chalcides ocellatus</i>	Squamata, Scincidae, Scincinae	0	0	0	0	generalist	Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Chalcides chalcides</i>	Squamata, Scincidae, Scincinae	0	0	0	0	grassy areas	Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019 IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Melanoseps ater</i>	Squamata, Scincidae, Scincinae	1	1	1	0	in litter	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Mesoscincus schwartzei</i>	Squamata, Scincidae, Scincinae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Mesoscincus managuae</i>	Squamata, Scincidae, Scincinae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Ophiomorus latastii</i>	Squamata, Scincidae, Scincinae	1	1	1	1	burrowin g	IUCN Red List; Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Ophiomorus punctatissimus</i>	Squamata, Scincidae, Scincinae	1	1	1	1	burrowin g	Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019 IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Brachymeles apus</i>	Squamata, Scincidae, Scincinae	1	1	1	1	burrowin g	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Brachymeles miriamae</i>	Squamata, Scincidae, Scincinae	1	1	1	1	burrowin g	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Brachymeles talinis</i>	Squamata, Scincidae, Scincinae	0	0	0	-	?	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Plestiodon multilineatus</i>	Squamata, Scincidae, Scincinae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Scincus mitranus</i>	Squamata, Scincidae, Scincinae	0	0	0	0	sandy dunes	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Hakaria simonyi</i>	Squamata, Scincidae, Scincinae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015

<i>Scelotes caffer</i>	Squamata, Scincidae, Scincinae	1	1	1	1	g	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Scelotes bipes</i>	Squamata, Scincidae, Scincinae	1	0	01	1	g	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Ameiva bifrontata</i>	Squamata, Teiidae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Teius teyou</i>	Squamata, Teiidae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Pholidobolus montium</i>	Squamata, Gymnophthal midae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Rhineura floridana</i>	Amphisbaenia, Rhineuridae	1	1	1	1	g	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Blanus cinereus</i>	Amphisbaenia, Blanidae	1	1	1	1	g	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Cadea blanoides</i>	Amphisbaenia, Cadeidae	1	1	1	1	g	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Bipes biporus</i>	Amphisbaenia, Bipedidae	0	1	01	1	g	IUCN Red List; Vitt & Caldwell, 2009; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Trogonophis wiegmanni</i>	Amphisbaenia, Trogonophida e	1	1	1	1	g	IUCN Red List; Vitt & Caldwell, 2009; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>† Slavoia darevskii</i>	Amphisbaenia	0	0	0	1	g	Talanda, 2016	Talanda, 2016
<i>Amphisbaena alba</i>	Amphisbaenia, Amphisbaenid ae	1	1	1	1	g	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Chirindia langi</i>	Amphisbaenia, Amphisbaenid ae	1	1	1	1	g	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Anomalepis mexicanus</i>	Serpentes, Anomalepidid ae	1	1	1	01	under trunk	IUCN Red List; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Leptotyphlops</i>	Serpentes, Leptotyphlopi dae	1	1	1	1	g	IUCN Red List	Da Silva <i>et al.</i> , 2018
<i>Indotyphlops braminus</i>	Serpentes, Typhlopidae	1	1	1	1	g	Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Xerotyphlops</i>	Serpentes,	1	1	1	1	g	IUCN Red	Da Silva <i>et</i>



<i>vermicularis</i>	Typhlopidae					g	List; Uetz <i>et al.</i> , 2019	<i>al.</i> , 2018
† <i>Dinlysia</i>	Serpentes	1	1	1	1	burrowing	Da Silva <i>et al.</i> , 2018	Da Silva <i>et al.</i> , 2018
† <i>Wonambi</i>	Serpentes	1	1	1	-	generalist ?	Palci <i>et al.</i> , 2018	Da Silva <i>et al.</i> , 2018
† <i>Yurlunggur</i>	Serpentes	1	1	1	1	semifossorial	Palci <i>et al.</i> , 2018	Da Silva <i>et al.</i> , 2018
							Maschio <i>et al.</i> , 2010;	
<i>Anilius scytale</i>	Serpentes, Aniliidae	1	1	1	1	burrowing	Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
† <i>Haasiophis</i>	Serpentes	1	1	1	1	burrowing	Da Silva <i>et al.</i> , 2018	Da Silva <i>et al.</i> , 2018
† <i>Pachyrhachis</i>	Serpentes	1	1	1	1	burrowing	Da Silva <i>et al.</i> , 2018	Da Silva <i>et al.</i> , 2018
<i>Tropidophis melanurus</i>	Serpentes, Tropidophiidae	1	1	1	1	burrowing	Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Casarea dussumieri</i>	Serpentes, Bolyeriidae	1	1	1	0	arboreal	IUCN Red List	Da Silva <i>et al.</i> , 2018
							Insacco <i>et al.</i> , 2015;	Reynolds <i>et al.</i> , 2014; Da
<i>Eryx jaculus</i>	Serpentes, Boidae	1	1	1	1	burrowing	Uetz <i>et al.</i> , 2019	Silva <i>et al.</i> , 2018
								Reynolds <i>et al.</i> , 2014; Da
<i>Boa constrictor</i>	Serpentes, Boidae	1	1	1	0	generalist	Uetz <i>et al.</i> , 2019	Silva <i>et al.</i> , 2018
								Reynolds <i>et al.</i> , 2014; Da
<i>Corallus hortulanus</i>	Serpentes, Boidae	1	1	1	0	arborical	IUCN Red List; Uetz <i>et al.</i> , 2019	Silva <i>et al.</i> , 2018
								Reynolds <i>et al.</i> , 2014; Da
<i>Eunectes murinus</i>	Serpentes, Boidae	1	1	1	0	shallow water	Uetz <i>et al.</i> , 2019	Silva <i>et al.</i> , 2018
							Gower <i>et al.</i> , 2008;	
<i>Uropeltis ceylanica</i>	Serpentes, Uropeltidae	1	1	1	1	burrowing	Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Python sebae</i>	Serpentes, Pythonidae	1	1	1	0	generalist	Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
								Wüster <i>et al.</i> , 2008; Da
<i>Crotalus horridus</i>	Serpentes, Viperidae	1	1	1	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Silva <i>et al.</i> , 2018
								Wüster <i>et al.</i> , 2008; Da
<i>Bitis arietans</i>	Serpentes, Viperidae	1	1	1	0	generalist	Uetz <i>et al.</i> , 2019	Silva <i>et al.</i> ,

								2018
<i>Macrovipera schweizeri</i>	Serpentes, Viperidae	1	1	1	0	rocky areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Wüster <i>et al.</i> , 2008; Da Silva <i>et al.</i> , 2018
<i>Daboia siamensis</i>	Serpentes, Viperidae	1	1	1	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Wüster <i>et al.</i> , 2008; Da Silva <i>et al.</i> , 2018
<i>Vipera ammodytes</i>	Serpentes, Viperidae	1	1	1	0	rocky areas	IUCN Red List; Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019	Wüster <i>et al.</i> , 2008; Da Silva <i>et al.</i> , 2018
<i>Vipera aspis</i>	Serpentes, Viperidae	1	1	1	0	generalist	IUCN Red List; Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019	Wüster <i>et al.</i> , 2008; Da Silva <i>et al.</i> , 2018
<i>Vipera berus</i>	Serpentes, Viperidae	1	1	1	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Wüster <i>et al.</i> , 2008; Da Silva <i>et al.</i> , 2018
<i>Micrurus nigrocinctus</i>	Serpentes, Elapidae	1	1	1	1	burrowing	IUCN Red List; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Hydrophis fasciatus</i>	Serpentes, Elapidae	1	1	1	0	coastal water	IUCN Red List; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Hydrophis cyanocinctus</i>	Serpentes, Elapidae	1	1	1	0	coastal water	IUCN Red List; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Naja atra</i>	Serpentes, Elapidae	1	1	1	-	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Naja senegalensis</i>	Serpentes, Elapidae	1	1	1	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Ophiophagus hannah</i>	Serpentes, Elapidae	1	1	1	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Macroprotodon cucullatus</i>	Serpentes, Colubridae	1	1	1	0	open habitats	IUCN Red List; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Calamaria albiventer</i>	Serpentes, Colubridae	1	1	1	1	burrowing, in litter	IUCN Red List; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018

<i>Coronella girondica</i>	Serpentes, Colubridae	1	1	1	0	generalist	IUCN Red List; Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Elaphe dione</i>	Serpentes, Colubridae	1	1	1	0	generalist	IUCN Red List; Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Eirenis modestus</i>	Serpentes, Colubridae	1	1	1	0	rocky areas	IUCN Red List; Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Hierophis viridiflavus</i>	Serpentes, Colubridae	1	1	1	0	open habitats	IUCN Red List; Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Natrix natrix</i>	Serpentes, Colubridae	1	1	1	0	humid, open habitats	IUCN Red List; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Virginia valeriae</i>	Serpentes, Colubridae	1	1	1	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Da Silva <i>et al.</i> , 2018
<i>Cordylus cordylus</i>	Squamata, Cordylidae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Ouroborus cataphractus</i>	Squamata, Cordylidae	0	0	0	0	rocky areas burrowing and grass-swimming	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Smaug giganteus</i>	Squamata, Cordylidae	0	0	0	1	g	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Cricosaura typica</i>	Squamata, Xantusiidae	0	0	0	0	wood	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Xantusia vigilis</i>	Squamata, Xantusiidae	0	0	0	0	arid areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Lacerta viridis</i>	Squamata, Lacertidae	0	0	0	0	generalist	IUCN Red List; Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015

							IUCN Red List; Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Podarcis muralis</i>	Squamata, Lacertidae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Takydromus sexlineatus</i>	Squamata, Lacertidae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Shinisaurus crocodilurus</i>	Squamata, Shinisauridae	0	0	0	0	semiaquatic	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Heloderma horridum</i>	Squamata, Helodermatidae	0	0	0	0	wood	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Varanus exanthematicus</i>	Squamata, Varanidae	0	0	0	0	agricultural areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Xenosaurus grandis</i>	Squamata, Xenosauridae Anguidae (Anniellidae secondo	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>†Ophisauriscus quadrupes</i>	Conrad <i>et al.</i> 2011)	0	0	0	1	burrowing	Sullivan <i>et al.</i> , 1999	Conrad <i>et al.</i> , 2011
<i>†Apodosauriscus minutus</i>	Squamata, Anniellidae	1	1	1	1	burrowing	Gauthier, 1982; Bell <i>et al.</i> , 1995	Conrad <i>et al.</i> , 2011
<i>Anniella pulchra</i>	Squamata, Anniellidae	1	1	1	1	burrowing	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Celestus enneagrammus</i>	Squamata, Diploglossidae	0	0	0	0	wood	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Diploglossus bilobatus</i>	Squamata, Diploglossidae	0	0	0	01	semi-fossorial	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Diploglossus pleii</i>	Squamata, Diploglossidae	0	0	0	1	burrowing, in litter	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Ophiodes intermedius</i>	Squamata, Diploglossidae	1	1*	1	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Ophiodes striatus</i>	Squamata, Diploglossidae	1	1	1	-	?	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Celestus agasepsoides</i>	Squamata, Diploglossidae	01	01	01	1	burrowing	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Celestus haetianus</i>	Squamata, Diploglossidae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Ophisaurus</i>	Squamata,	1	1	1	01	semi-	IUCN Red	Reeder <i>et al.</i> ,

<i>ventralis</i>	Anguidae					fossorial	List; Uetz <i>et al.</i> , 2019 IUCN Red List;	2015
<i>Anguis fragilis</i>	Squamata, Anguidae	1	1	1	1	burrowing and grass-swimmer	Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Pseudopus apodus</i>	Squamata, Anguidae	1	1	1	1	grass-swimmer	Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Elgaria multicarinata</i>	Squamata, Anguidae	0	0	0	0	generalist	Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Abronia oaxacae</i>	Squamata, Anguidae	0	0	0	0	arboreal	Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Barisia levicollis</i>	Squamata, Anguidae	0	0	0	0	wood	Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Gerrhonotus parvus</i>	Squamata, Anguidae	0	0	0	0	wood	Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Chamaeleo chamaeleon</i>	Squamata, Chamaeleonidae	0	0	0	0	arboreal	Speybroeck <i>et al.</i> , 2016; Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Uromastyx aegyptia</i>	Squamata, Agamidae	0	0	0	0	open habitats	Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Agama spinosa</i>	Squamata, Agamidae	0	0	0	0	rocky areas	Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Draco cornutus</i>	Squamata, Agamidae	0	0	0	0	arboreal	Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Hydrosaurus amboinensis</i>	Squamata, Agamidae	0	0	0	0	semiaquatic	Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Basiliscus basiliscus</i>	Squamata, Iguanidae (s.l.), Corytophanidae	0	0	0	0	semiaquatic	Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015
<i>Anolis proboscis</i>	Squamata, Iguanidae (s.l.), Dactyloidae	0	0	0	0	arboreal	Uetz <i>et al.</i> , 2019 IUCN Red List;	Reeder <i>et al.</i> , 2015

<i>Iguana delicatissima</i>	Squamata, Iguanidae (s.l.), Iguanidae (s.s.)	0	0	0	0	arboreal	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Phrynosoma asio</i>	Squamata, Iguanidae (s.l.), Phrynosomatidae	0	0	0	0	generalist	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Leiocephalus carinatus</i>	Squamata, Iguanidae (s.l.), Leiocephalidae	0	0	0	0	rocky areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Polychrus gutturosus</i>	Squamata, Iguanidae (s.l.), Polychrotidae	0	0	0	0	arboreal	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Enyaliodes heterolepis</i>	Squamata, Iguanidae (s.l.), Hoplocercidae	0	0	0	0	wood	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Leiosaurus catamarcensis</i>	Squamata, Iguanidae (s.l.), Leiosauridae	0	0	0	0	wood	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Oplurus saxicola</i>	Squamata, Iguanidae (s.l.), Opluridae	0	0	0	0	rocky areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Liolaemus anomalus</i>	Squamata, Iguanidae (s.l.), Liolaemidae	0	0	0	0	arid, salty areas	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
<i>Tropidurus torquatus</i>	Squamata, Iguanidae (s.l.), Tropiduridae	0	0	0	0	wood	IUCN Red List; Uetz <i>et al.</i> , 2019	Reeder <i>et al.</i> , 2015
† <i>Eocaecilia micropodia</i>	Gymnophiona	0	0	0	1	burrowin g	Jenkins <i>et al.</i> , 2007	Evans & Sigogneau-Russell, 2011
<i>Epicrionops marmoratus</i>	Gymnophiona	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Epicrionops niger</i>	Gymnophiona	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Rhinatrema bivittatum</i>	Gymnophiona	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Uraeotyphlus natayani</i>	Gymnophiona	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Ichthyophis bombayensis</i>	Gymnophiona	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Ichthyophis tricolor</i>	Gymnophiona	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011

<i>Ichthyophis orthoplicatus</i>	Gymnophiona	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Ichthyophis glutinosus</i>	Gymnophiona	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Ichthyophis bannanicus</i>	Gymnophiona	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Caecilia tentaculata</i>	Gymnophiona	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Cryptobranchius</i>	Cryptobranchiidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>alleganiensis</i>		0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Onychodactylus fischeri</i>	Hynobiidae	0	0	0	0	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Pseudobranchius striatus</i>	Sirenidae	0	1	01	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Pseudobranchius axanthus</i>	Sirenidae	0	1	01	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Siren intermedia</i>	Sirenidae	0	1	01	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Siren lacertina</i>	Sirenidae	0	1	01	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Dicamptodon tenebrosus</i>	Dicamptodontidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Ambystoma cingulatum</i>	Ambystomidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Salamandrina terdigitata</i>	Salamandridae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Chioglossa lusitanica</i>	Salamandridae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Salamandra lanzai</i>	Salamandridae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Proteus anguinus</i>	Proteidae	0	0	0	1	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Necturus lewisi</i>	Proteidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Necturus punctatus</i>	Proteidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Necturus beyeri</i>	Proteidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Necturus alabamensis</i>	Proteidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Necturus maculosus</i>	Proteidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Rhyacotriton kezeri</i>	Rhyacotritonidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Rhyacotriton variegatus</i>	Rhyacotritonidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Amphiuma tridactylum</i>	Amphiumidae	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Amphiuma pholeter</i>	Amphiumidae	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Amphiuma means</i>	Amphiumidae	1	1	1	1	burrowin g	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Hydromantes</i>	Plethodontinae	0	0	0	0	generalist	Amphibia	Pyron & Wiens, 2011

<i>shastae</i>							Web, 2019	Wiens, 2011
<i>Ensatina</i>							Amphibia	Pyron &
<i>eschschollzii</i>	Plethodontinae	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Desmognathus</i>							Amphibia	Pyron &
<i>s carolinensis</i>	Plethodontinae	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Plethodon</i>							Amphibia	Pyron &
<i>larselli</i>	Plethodontinae	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Hemidactyliu</i>	Hemidactylina						Amphibia	Pyron &
<i>m scutatum</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Gyrinophilus</i>							Amphibia	Pyron &
<i>porphyriticus</i>	Spelerpinae	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Eurycea</i>							Amphibia	Pyron &
<i>multiplicata</i>	Spelerpinae	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Haideotriton</i>							Amphibia	Pyron &
<i>wallacei</i>	Spelerpinae	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Euricea</i>							Amphibia	Pyron &
<i>quadridigitata</i>	Spelerpinae	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Batrachoseps</i>	Bolitoglossina						Amphibia	Pyron &
<i>wrighti</i>	e	0	0	0	1	generalist	Web, 2019	Wiens, 2011
<i>Batrachoseps</i>	Bolitoglossina						Amphibia	Pyron &
<i>diabolicus</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Batrachoseps</i>	Bolitoglossina						Amphibia	Pyron &
<i>gabrielii</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Batrachoseps</i>	Bolitoglossina						Amphibia	Pyron &
<i>pacificus</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Batrachoseps</i>	Bolitoglossina						Amphibia	Pyron &
<i>attenuatus</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Batrachoseps</i>	Bolitoglossina						Amphibia	Pyron &
<i>nigriventris</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Thorius</i>	Bolitoglossina						Amphibia	Pyron &
<i>minutissimus</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Thorius</i>	Bolitoglossina						Amphibia	Pyron &
<i>trogodytes</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Thorius</i>	Bolitoglossina						Amphibia	Pyron &
<i>dubitus</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Chiropterotrit</i>	Bolitoglossina						Amphibia	Pyron &
<i>on dimidiatus</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Dendrotriton</i>	Bolitoglossina						Amphibia	Pyron &
<i>rabbi</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Cryptotriton</i>								
<i>alvarezdeltoro</i>	Bolitoglossina						Amphibia	Pyron &
<i>i</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Nototriton</i>	Bolitoglossina						Amphibia	Pyron &
<i>brodiei</i>	e	0	0	0	0	litter	Web, 2019	Wiens, 2011
<i>Bradytriton</i>	Bolitoglossina						Amphibia	Pyron &
<i>silus</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Oedipina</i>	Bolitoglossina						Amphibia	Pyron &
<i>quadra</i>	e	0	0	0	0	litter	Web, 2019	Wiens, 2011
<i>Oedipina</i>	Bolitoglossina						Amphibia	Pyron &
<i>carablanca</i>	e	0	0	0	0	generalist	Web, 2019	Wiens, 2011
<i>Oedipina</i>	Bolitoglossina						Amphibia	Pyron &
<i>elongata</i>	e	0	0	0	0	litter	Web, 2019	Wiens, 2011
<i>Oedipina</i>	Bolitoglossina						Amphibia	Pyron &
<i>maritima</i>	e	0	0	0	0	litter	Web, 2019	Wiens, 2011



<i>Oedipina alleni</i>	Bolitoglossina e	0	0	0	0	litter	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Oedipina stenopodia</i>	Bolitoglossina e	0	0	0	0	litter	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Oedipina gracilis</i>	Bolitoglossina e	0	0	0	0	litter	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Parvimolge townsendi</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Pseudoeurycea a cephalica</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Pseudoeurycea a boneti</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Pseudoeurycea a gigantea</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Lineatriton lineolus</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Pseudoeurycea a firscheini</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Pseudoeurycea a obesa</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Pseudoerycea melanomolga</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Bolitoglossa hartwegi</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Bolitoglossa platydactyla</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Bolitoglossa subpalmata</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
<i>Bolitoglossa alvaradoi</i>	Bolitoglossina e	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011

### Appendix 3. References cited in Appendix 1 and 2.

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